IRON NUTRITION AND DEFICIENCY: A REVIEW WITH EMPHASIS IN AVOCADO (*Persea americana* Mill.)

S. Salazar-García
INIFAP-Campo Experimental Santiago Ixcuintla, Apdo. Postal 100, Santiago Ixcuintla, Nay. 63300, México. Tel./Fax: (323)5-0710 E-mail: ssalazar@tepic.edi.com.mx

SUMMARY

Avocados are susceptible to iron deficiency, and the ideal pH to grow them satisfactorily is 5.5 to 6.5. Conditions higher than pH 7 will probably cause iron deficiency. The symptomatology of iron deficiency is usually manifested as an interveinal chlorosis of young leaves while the veins remain green -hence the name iron deficiency chlorosis. Research on metabolism, biochemistry and physiology of iron in plants and avocado is discussed as well as approaches to control iron deficiency chlorosis in avocado. The best method to avoid iron deficiency would be to avoid planting avocados on highly calcareous soils, or to use rootstocks which are resistant to lime-induced chlorosis, on the other hand, several strategies have been developed to alleviate the problem of iron chlorosis. Apparently the only possibility to control iron chlorosis in established orchards is by soil applications of Fe chelates, since applications by foliar sprays have not been successful on a commercial scale. In the long term, development and use of avocado rootstocks with tolerance to calcareous soils or more Fe-efficient cultivars still seems to be the most economical solution to permanently control Fe chlorosis

KEY WORDS: Chlorosis, iron uptake, deficiency correction.

NUTRICIÓN Y DEFICIENCIA DE HIERRO, UNA REVISIÓN CON ÉNFASIS EN AGUACATERO (*Persea americana* Mill.)

RESUMEN

Como el aguacatero es muy susceptible a la deficiencia de hierro el pH ideal para su cultivo es entre 5.5 y 6.5. Cuando el pH es superior a 7, es muy probable que ocurran deficiencias de hierro ya que el calcio es el catión predominante en ese tipo de suelos. El resultado de estas condiciones es una clorosis por suelos calcáreos, la cual a nivel mundial, es posiblemente más importante en aguacatero que en cualquier otro frutal. Los síntomas de deficiencia de hierro normalmente se manifiestan en forma de clorosis intervenales en hojas jóvenes, mientras que las nervaduras permanecen verdes, de aquí el nombre de clorosis férrica. En esta revisión se presenta y discute la investigación realizada sobre el metabolismo, bioquímica y fisiología del hierro en las plantas, especialmente en aguacatero, así como medidas para controlar la clorosis férrica en aguacatero El mejor método para evitar la clorosis férrica es no establecer aguacateros en suelos muy calcáreos o usar portainjertos tolerantes a la clorosis causada por los suelos calcáreos. Existen algunas estrategias para reducir el problema de la clorosis férrica. Aparentemente la única posibilidad para controlar la clorosis férrica en huertos de aguacatero es mediante la aplicación al suelo de quelatos de hierro, ya que las aspersiones foliares no han funcionado con propósitos comerciales. Como una medida de control permanente, parece ser que la solución más económica para controlar la clorosis férrica del aguacatero es el desarrollo y uso de portainjertos tolerantes a suelos calcáreos o el disponer de cultivares con mejor aprovechamiento del hierro.

PALABRAS CLAVE: Clorosis, absorción de hierro, corrección de deficiencias.

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IRON CHLOROSIS: OVERVIEW AND DEFINITION

The historical record of research on iron-deficiency chlorosis can be partitioned into three broad phases (Korcak,1987): i) mid-1800s to early 1900s, research centered on observations of chlorotic plants and the establishment of the association with iron supply, ii) post-World War II to 1970s, a dual approach, the formulation and use of synthetic chelating agents in correcting iron deficiency chlorosis, and concentration on species and cultivar differences in the efficiency of iron uptake, iii) the role of the rhizosphere (pH modification and exudates) in iron-stress response and the physiology and biochemistry of iron uptake in plants. This review will touch upon all three of these phases and concentrate on fruit tree crops, in particular, avocado.

Classical role in plants

Iron is an important component of enzymes involved in the transfer of electrons (redox reactions such as cytochromes and iron-sulfur (FeS) proteins); also it is a constituent of nonheme iron proteins involved in photosynthesis, N_2 fixation, and respiration (Taiz and Zeiger, 1991). In this role it is reversibly oxidized from Fe^{2+} to Fe^{3+} during electron transfer. As in Mg deficiency, characteristic symptoms of iron deficiency involve interveinal chlorosis. However, because iron cannot be readily mobilized from older leaves, these symptoms occur initially on the younger leaves. Under conditions of extreme or prolonged deficiency, the whole leaf may become white. Chlorosis on the leaves occurs because iron is required for chlorophyll synthesis. However, the precise role of iron in chlorophyll synthesis is still a subject of research. The low mobility of iron is probably due to precipitation in the older leaves as insoluble oxides or phosphates or to the formation of complexes with phytoferritin, an iron-binding protein found in the leaf (Bienfait and Van der Mark, 1983). The precipitation of iron reduces its subsequent mobilization to the phloem for long-distance translocation.

Definition

Iron deficiency can occur at both extremes of the pH range of agricultural soils. The following factors may contribute either singly or in combination to the development of chlorosis: low iron supply; calcium carbonate in soil; bicarbonate in soil or irrigation water; over irrigation or waterlogged conditions; high phosphate levels; high levels of heavy metals; low or high temperatures; high light intensities; high levels of nitrate nitrogen; imbalances in cation ratios; poor soil aeration; certain organic matter additions to soil; viruses; root damage by nematodes and other organisms (Wallace and Lunt, 1960; Embleton *et al*., 1973).

Iron deficiency is usually manifested as an interveinal chlorosis of young leaves while the veins remain green, hence the name iron-deficiency chlorosis. The expression of the symptoms in young leaves is due to the inability to redistribute iron within the plant. Iron may, however, become more mobile under stress conditions (Price, 1968). During a new flush of vegetative growth in 'Tahiti' lime, the symptoms of chlorosis shifted to the newly formed leaves with a corresponding regreening of the previous flush (Davenport, 1983). Mango trees express atypical lime-induced chlorosis symptoms: initially the entire young leaf blade turns yellowish green, it eventually ceases growth, and the branch gradually dies back (Kadman and Gazit, 1984). Grapefruit tended to develop an unidentified gummosis on main limbs under iron-deficiency stress (Horesh and Levy, 1981). In avocado, the iron-deficiency symptoms may differ in severity (Kadman and Cohen, 1973-74). In light cases, chlorosis may hardly be recognized. In severe cases the trees not only present an acute chlorosis but lose most of their leaves and experience a generalized die-back of shoots (Wallace and Lunt, 1960; Embleton and Jones, 1966). Fruit from iron-deficient avocado trees may be of reduced quality due to yellowish skin (Malo, 1965).

Chlorosis is often a useful indicator of iron content or its activity in avocado leaves. Increased chlorosis was related to decreased leaf Fe, chlorophyll, and catalase activity of young leaves when avocado seedlings were grown in increasing levels of $CaCO_3$ in soil (5 to 30%) (López-Jiménez, 1985).

The expression of iron chlorosis may be confused with the occurrence of simultaneous micronutrient deficiencies, as with zinc and iron (Dixit and Yamdagni, 1983) and manganese, iron and zinc in citrus (Bar-Akiva and Lavon, 1968) and apple (Shen and Tseng, 1949). To distinguish chlorosis due to iron deficiency alone and to provide a workable diagnosis of the disorder, the definition of iron-deficiency chlorosis presented by Chaney (1984) is most appropriate: any yellowing of leaves that regreens when treated with $FeSO_4$ or FeEDDHA (ethylenediaminedi-o-hydroxyphenylacetic acid), but does not regreen when nitrogen, sulfur, zinc, manganese, copper, cobalt, or other nutrients are applied alone or in combination.

UPTAKE BY ROOTS

The primary, if not the sole, form in which iron is absorbed by plants (except gramineous monocots) is Fe^{2+} (Chaney *et al*., 1972). Since the primary form of iron in most agricultural soils is Fe^{3+} (except for flooded rice), plants must solubilize Fe^{3+} and then reduce it to Fe^{2+} for absorption or transport into the root. Plant iron uptake requires energy (Moore, 1972), and both oxygen and photosynthetic substrates are required for iron reduction by roots in apple (Tong *et al*., 1985). The exact area in, on, or near the root where this reduction takes place is unknown (Römheld and Marschner, 1985). The root section between 1 and 4 cm from the tip in barley absorbed and translocated more iron than the rest of the root (Clarkson and Sanderson, 1978). Roots of grape rootstocks under iron stress displayed enhanced proton release from approximately the same area (Korcak, 1987).

Based on qualitative differences, Römheld and Marschner (1985, 1986) have proposed that iron uptake occurs by two species-dependent strategies. Iron mobilization by dicots and nongramineous monocots in response to iron deficiency stress is termed strategy I, and that found only with gramineous monocots is called strategy II. The chemotaxonomic boundary for the two strategies is not between dicotyledons and monocotyledons, but between most higher plants and grasses (Graminaceae) (Römheld, 1987).

Plant species exhibiting strategy I show one or more of the following adaptive components: i) an iron deficiency-induced enhancement of Fe^{3+} reduction to Fe^{2+} at the root surface, with preferential uptake of Fe^{2+} (Chaney *et al.*, 1972), ii) H^+ extrusion (Römheld and Marschner, 1984), which promotes the reduction of Fe^{3+} to Fe^{2+}, and iii) in certain cases the release of reducing and/or chelating substances by the roots (Hether *et al.*, 1984). Enhanced Fe^{3+} reduction under iron-deficiency, the most typical feature of strategy I, is characterized by the activation of "reductases" located on the plasma membrane and presumably in the cell wall (apoplast) of apical root zones (Bienfait *et al.*, 1983). Net Fe^{3+} reduction is strongly impaired at high pH due to inhibited "reductase" and auto oxidation of Fe^{2+}. As a consequence, plant species exhibiting strategy I often display chlorosis symptoms when grown on alkaline (calcareous) soils, especially at high HCO_3^- concentrations and corresponding strong pH-buffering capacities. The efficiency of this strategy depends on the supply of soluble iron (mainly iron chelates) to the reductase system.

Strategy II systems are characterized by an iron-deficiency-induced release of specific Fe^{3+}-chelating compounds ("phytosiderophores"; Takagi *et al.*, 1984) and a high affinity uptake system (transport protein) for Fe^{3+} phytosiderophores (Römheld and Marschner, 1986). As a consequence, gramineous species exhibiting these two components are highly efficient at acquiring iron from sparingly soluble inorganic Fe^{3+} (e.g. iron hydroxide). This is in contrast to species with strategy I.

In grafted plants, the root system has shown a dominant effect on iron absorption. In grafting experiments with Fe-efficient and Fe-inefficient tomato (Brown *et al.*, 1971) and soybean (Brown *et al.*, 1958), the roots controlled development of Fe-efficiency reactions: Only those grafts with the roots from the Fe-efficient variety showed normal iron uptake. However, the control is not necessarily located exclusively in the roots. Chlorotic leaves might send a signal to the roots inducing them to develop the reactions; only the roots of efficient varieties could pick up and interpret the "chlorosis signal".

TRANSLOCATION FROM ROOTS TO SHOOTS

Iron is translocated from roots to shoots as a ferric-citrate chelate (Tiffin, 1972). This is transported to actively growing shoot regions (Bennett *et al.*, 1982). In iron-stressed pears (Oserkowsky, 1932) and silver plate (Morris and Swanson, 1981) the pH of the xylem sap did not differ from that of non-stressed plants. The latter authors also showed that iron stress did not change the redox potential of the sap compared to that of non-stressed trees. Since iron moves as a citrate complex, its stability during transport would be determined, in part, by both pH and redox potential. Thus, under iron stress, movement as a citrate-chelate should not be affected. Translocation via citrate in stem exudates of four soybeans genotypes was most nearly related to the available iron supply (Brown *et al.*, 1958).

FOLIAR UPTAKE

The following three conditions significantly affect iron foliar uptake:

I) The availability of the micronutrient on the leaf surface, which is directly related to the water solubility of applied compounds and also depends on external factors such as humidity and temperature. The precipitation or crystallization of the exogenous element leads to its immobilization. The higher retention of inorganic iron in epicuticular waxes may be connected with its low solubility. Indeed, Fe^{2+} solubility extends over a wide pH range, but this element is readily oxidized to Fe^{3+}, which tends to precipitate out in the form of hydroxide even at low pH (Williams, 1981). The formation of such an insoluble product would immobilize the element on the leaf surface. Chelating improves iron solubility in water (Aboulroos *et al.*, 1983; Hellin *et al.*, 1987); this property can explain the lesser superficial retention and consequently the higher uptake with chelates.

II) The passage through the cuticle. Iron and zinc cross the cuticle of pea plants more readily as free ions (Ferrandon, 1988, cited by Ferrandon and Chamel, 1989), although an opposite result occurred with iron in citrus (Basiouny and Biggs, 1976). Penetration of substances through the cuticle is a diffusive process influenced by temperature and by concentration gradient. Water and solutes penetrate through both stomatous and astomatous cuticles (Yamada *et al.*, 1964). Penetration through stomatous cuticles is usually more rapid than through astomatous cuticles (Chamel, 1980), although citrus cuticle shows the opposite (Basiouny and Biggs, 1976).

Cuticles are 10 to 20 times more permeable to urea than to inorganic ions (Yamada *et al.*, 1965). Addition of nitrogen compounds to the sprays can enhance iron uptake. In corn, the addition of urea and ammonium nitrate increased the effectiveness of foliar-applied $FeSO_4$ (Hsu and Ashmead, 1984); urea and ammonium nitrate had no effect on Fe-amino chelate but decreased the effectiveness of Fe-EDTA.

l) The absorption by underlying tissues. The absorption of nutrients by plant leaves may be similar to that by roots (Kannan, 1980), the main step being the transport through the plasmalemma. As transport through the plasmalemma is an active process, for most plant nutrients, the uptake rate is influenced by the physiological status of the leaf (Mengel and Kirkby, 1987). In leaf tissues, in contrast to the root, this active uptake process is usually not the limiting step in ion uptake. The rate of uptake is controlled by the diffusion of plant nutrients from the water film on the leaf surface (which is usually higher than in the soil solution) through the cuticle and cell material to the plasmalemma. The foliar absorption process is energy-dependent and is coupled to oxidative phosphorylation. In the light, energy for leaf absorption may be alternatively supplied by photophosphorylation (Robinson and Smith, 1970).

TRANSLOCATION OF FOLIAR APPLIED IRON

According to Bukovac and Wittwer (1957), iron is classified as a partially mobile nutrient. However, as much as 60% of foliar-absorbed ^{59}Fe (from $^{59}FeCl_3$) might be translocated out of the leaf within 50 hours in sorghum (Eddings and Brown, 1967). In tomato and white beans the transport was not as efficient but involved at least 25% of leaf absorbed ^{59}Fe. Translocation of foliar-applied Fe may be enhanced by chelation and by treatment with GA_3 or kinetin (6-furfurylamino purine) (Kannan and Mathew, 1970). In corn applying sulfate with chelating agents (EDTA, EDDHA, or DTPA) considerably increased translocation of iron out of the treated leaf (Ferrandon and Chamel, 1989). These authors suggest that the metal cation is bound to its ligand within the plant and that its high mobility might correspond to a lesser affinity of chelated iron for the negative sites on cell membranes and along vessels.

BIOCHEMISTRY, METABOLISM, AND PHYSIOLOGY

The tendency for iron to form chelates and its ability to undergo a valence change ($Fe^{2+} \Leftrightarrow Fe^{3+} + e^-$) are the two important characteristics underlying its numerous physiological effects. The best known function of Fe is in enzyme systems in which haem or haemin function as prosthetic groups (Mengel and Kirkby, 1987). Here, iron plays a somewhat similar role to Mg in the porphyrin structure of the chlorophyll. These haem enzyme systems include catalase, peroxidase, cytochrome oxidase as well as the various cytochromes. The role of these enzymes in plant metabolism is not completely understood. More is known of the function of the cytochromes in electron transport and the involvement of cytochrome oxidase in the terminal step of the respiration chain. Catalase brings about the breakdown of H_2O_2 to water and ½ O_2. This enzyme also plays an important role in the chloroplasts along with the enzyme superoxide dismutase, and in photorespiration and the glycolytic pathway.

Cell-wall-bound peroxidases appear to catalyze a reaction in the polymerization of phenols to lignin. Peroxidase activity seems to be particularly depressed in Fe-deficient roots. Cell-wall formation and lignification were impaired and phenolics accumulated in the rhizodermis of Fe-deficient sunflower roots (Römheld and Marschner, 1981). Phenolics can be released into the external solution (Olsen *et al*., 1981), and in the case of caffeic acid may bring about chelation and reduction of inorganic Fe^{3+}. This reaction is favored not only by the accumulation of phenolics but also by an increase in the reducing capacity of the roots which accompanies the impairment of lignin synthesis.

Although highly important in metabolism, the haem pigments constitute only about 0.1% of the total iron in plant leaves (Dekock *et al*., 1960). The remaining iron is stored largely as phytoferritin, a ferric phosphoprotein. Hyde *et al*. (1963) have proposed that phytoferritin in leaves represents an Fe reserve used by developing plastids for photosynthetic needs. Barton (1970) observed large quantities of phytoferritin in chloroplasts, confirming earlier evidence that chloroplasts are rich in Fe, containing as much as 80% of the total Fe in plants (Neish, 1939).

Like haem Fe, iron sulfur proteins play a major role in oxidoreduction. Both binuclear Fe-S clusters (2Fe-2S) and tetranuclear Fe-S clusters (4Fe-4S) occur. Each cluster is surrounded by four cysteine residues associated to a polypeptide chain (Sandmann and Böger, 1983). These clusters are known as ferredoxins if they act exclusively as electron carriers and are characterized by a very high negative redox potential.

In green plants iron and chlorophyll concentrations are often well correlated. The same metabolic pathway involved in chlorophyll formation also operates in the biosynthesis of haem . Iron appears to control the rate of formation of delta-amino-laevulinic acid (ALA), the precursor of porphyrins (Miller *et al*., 1980). In Fe deficiency, a decrease occurred in the rate of condensation of glycine and succinyl CoA to form ALA. In Fe-deficient leaves, the photosynthetic apparatus remained intact, but the number of photosynthetic units decreased (Terry, 1980).

Iron is probably involved in protein metabolism. In Fe deficiency the protein fraction decreases simultaneously with an increase in the level of soluble organic N compounds (Bennet, 1945; Perur *et al*., 1961). In Fe-deficient fruit tree leaves, for example, Iljin (1951) found protein contents about half those of healthy leaves. From short-term experiments on the alga *Euglena gracilis,* iron appears to be directly implicated in nucleic acid metabolism (Price *et al*., 1972).

DISEASE AND INSECT PEST INTERACTIONS

Siderophores can affect plant life in at least three ways. In the first, the chelates act in the soil to solubilize and transport Fe^{3+}. Since microorganisms preceded plants in the evolutionary succession, it is reasonable to suppose that the former life forms played, and continue to play, a role in weathering of rocks and formation of soil. It is further reasonable to imagine that plants adapted their iron transport systems so as to exploit those already devised by microorganisms. Although certain siderophores have been found to be effective sources of iron for higher plants, a specific transport system for ferrisiderophores has yet to be demonstrated outside of the microbial world (Neilands and Leong, 1986).

A second possible effect of siderophores may be the facilitation of plant disease. Siderophores are one very important determinant of virulence for infections of animals. The situation is less clear cut in plants, but iron status of the host and relative capacity of the pathogen to acquire iron may similarly influence the course of infection and disease (Neilands and Leong, 1986).

The third mechanism is biocontrol in which certain microbial species, such as fluorescent pseudomonads, discourage the growth or metabolic activities of competing microorganisms. Siderophores appear to play some part in this process. Antibiosis, hormone effects, and lytic activity may work in combination with siderophores to afford a microenvironment at the root surface that favors or impedes plant growth (Neilands and Leong, 1986).

Iron deficiency can also affect the suitability of plants for insect establishment. Oviposition rate of the mustard beetle (*Phaedon cochleariae* F.) declined as Fe concentration decreased in watercress (*Nasturtium officinale* L.) leaves (Allen and Selman, 1957). Both low and high levels of Fe significantly reduced plant growth and biomass and resistance to whitebacked planthopper (*Sogatella furcifera*) in two rice varieties (Salim and Saxena, 1992). Fe stress apparently decreased only the quantity of allelochemicals produced but did not alter their nature or quality, which is hereditarily predetermined and not subject to external influences.

Little information is available on the effect of iron nutrition on any avocado disease or pest related problem. However, some inferences can be made. For example, foliar levels of Fe in avocado trees affected by *Phytophthora cinnamomi* Rands decreased with soil application of the fungicide Metalaxyl (Núñez-Moreno *et al*., 1991). This effect could be caused by a decrease of the natural soil mycorrhizal fungi population. Besides increasing phosphorus absorption by avocado roots (Ferrera-Cerrato, 1994)*, mycorhizae also increased the absorption of Co, Cu, and Fe (Mosse *et al*., 1976). In alkaline soils iron deficiency can increase the avocado susceptibility to insect attack, possibly due to an attracting effect of the yellowish color of iron-deficient chlorotic plants. In avocado trees, a chlorotic appearance has been related with a higher incidence of the branch weevil (*Copturus aguacatae* Kiss.) (Cabrera-Bautista and Salazar-García, 1991). Many years of improper nutrition management in Atlixco, Puebla, Mexico, have produced thousands of chlorotic trees that are being severely attacked by the branch weevil (Salazar-García and Bolio-García, 1992).

STRATEGIES TO CONTROL IRON DEFICIENCY CHLOROSIS IN AVOCADO

The ideal pH for avocado trees is 5.5 to 6.5. Avocados are susceptible to iron deficiency at pH greater than 7 because calcium is the dominant cation in such soils. The resulting lime-induced chlorosis is perhaps more critical to avocados on a worldwide scale than to any other fruit crop (Malo, 1976). Most tropical and subtropical commercial avocado areas, particularly the drier ones, have a high incidence of neutral to alkaline soils where Fe chlorosis is a major problem.

Soil applications

Even when salts of iron such as iron sulfate are liberally applied to alkaline soils, plants are not always able to utilize them. Several factors contribute to this problem. Under alkaline conditions, iron rapidly forms insoluble iron hydroxide and carbonate complexes (Wallace, 1962). It is also rapidly oxidized to form insoluble iron oxide (rust), and the calcium in calcareous soils and/or magnesium in dolomitic soils competes with iron for uptake into the plant. All of these factors make the percent of soluble iron (Fe^{2+}) in soils extremely low. Other heavy metals, such as copper, when present in high enough concentration, as a result of fungicidal spraying, will cause iron deficiency symptoms (Leonard and Stewart, 1952).

Chelated materials have been used to protect Fe^{2+} from attack by precipitating and oxidizing agents in the soil. Because this strategy has met with the greatest success, it has become the most popular approach to iron nutrition in highly alkaline soils. Chelation is defined as a coordination in which a ring structure is formed between the chelator and metal (Wallace, 1962). The greater the number of coordinated bonds that exist in a chelate complex, up to six (the number of coordinate points of

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*Personal communication. Dr. Ronald Ferrera-Cerrato, Colegio de Postgraduados, Montecillo, Edo. de Mex.

iron), the more stable the compound. The greater the stability of soluble iron chelate complex the most likely is to resist precipitation by the prevalent hydroxide and/or carbonate ions, thereby maintaining a high concentration in the soil. The logarithm of the stability constants of some common commercial chelators are: EDTA (ethylenediamine tetracetic acid) = 25.1, DTPA (diethylenetriamine pentacetic acid) = 28.6, and EDDHA [ethylenediamine (di o-hydroxiphenil acetic acid)] = 33.0. Each unit of difference in these values represents a 10-fold difference in stability; for example, the difference between EDTA and EDDHA is approximately 8 which means EDDHA is 100 million times (10^8) more stable than EDTA.

FeEDTA, the first synthetic chelate used in agriculture (Leonard and Stewart, 1952), can be used successfully in acid soils . In neutral or basic soils is hydrolyzed and Fe substituted by calcium (Sánchez *et al*., 1991). The most effective chelate for curing iron chlorosis in avocado in acid and alkaline soils is FeEDDHA (commercial name Sequestrene 138-Fe) . This chelate is stable from pH 4 to 10, whereas the stability of FeEDTA decreases above pH 7.

In pot-grown avocado seedlings of eight different varieties in highly calcareous soil (about 65% $CaCO_3$), chlorosis symptoms completely disappeared three weeks after application of 5 g of Chel. 138 HFe (HFe EDDHA) to the soil (Kadman, 1962). Similar results were obtained by Kadman when 30 g of Chel. 138-Fe per tree were applied in a commercial orchard. The symptoms of chlorosis disappeared in two months and did not reappear in two years. Soil injections with other Fe-chelates showed less striking effects (Kadman and Lahav, 1971-72). Soil application of 150 g Sequestrene 138-Fe per tree to avocado in Cyprus not only eliminated the visual symptoms of chlorosis for a long time but also increased both growth and yield when compared with other iron treatments and the control (Gregoriou *et al*., 1983). The optimum rate of chelates depends on tree size, degree of chlorosis, soil type, and management practices and should be determined experimentally in each location. The success of a low application level of chelate would depend upon an effective means of application. Unfortunately, the most stable chelates tend to be too expensive for commercial use, and their effect normally disappears after six months (Bingham and Beutel, 1957); however, grower use and experience are the most critical criteria of cost effectiveness.

Foliar sprays

Because soil applications of most of Fe sources generally are ineffective, foliar sprays are thought to be a viable alternative to correct iron chlorosis. Foliar sprays can be an important alternative to correct iron deficiency in those areas or orchards under unwatered (rainfed) conditions. Foliar sprays usually need to be repeated periodically, such as every two or three weeks. The cost of materials is not great, but the cost of labor is high.

Foliar sprays of $FeSO_4$ or $Fe(NO_3)_2$ corrected Fe chlorosis of mango trees with inclusion of a surfactant (Kadman and Gazit, 1984). Spray applications of some linosulfonates to pear trees corrected Fe chlorosis, but only for the season of application (Raese *et al.,* 1986). Foliar sprays of ferric citrate plus NH_4NO_3, $FeSO_4$, and FeDTPA partially corrected Fe chlorosis on peaches and grapes (Reed *et al*., 1988). In avocado, little information on the correction of iron chlorosis by foliar sprays is available. Embleton and Jones (1966) and Kadman and Lahav (1971-72) mention a lack of response of avocado trees and the occasional detection of leaf burn. The latter result was probably due to the exclusion of surfactants, although the pH of the sprayed solution was not mentioned.

There is much controversy on the absorption of foliar-applied Fe products. Some times a higher dose (e.g. 1 to 2% $FeSO_4 \cdot 7H_2O$) can compensate for a low absorption rate; however, these high levels of Fe can result in burned leaf margins and severe phytotoxicity. Development of superior non-toxic surfactants that enhance penetration of iron into stomatal openings of leaves has increased the potential for new approaches to iron nutrition in fruit crops (Newman and Prinz, 1974a, b). New evaluations on the response of iron chlorotic avocado trees to sprays of chelates plus surfactants will be necessary. Leaves do not have an acid-producing mechanism as do roots; so there are at least two advantages for supplying foliar Fe at a pH on the low side of the physiological range. Lower Fe concentrations may be used, which decreases risk of phytotoxicity, and the Fe may be more readily available for leaf absorption. Macadamia responded well to foliar sprays of $FeSO_4$ at pH 3, 2, and 1 (Wallace and Bedri, 1958). Leaves of many species will not tolerate pH 1, but most will tolerate pH 3. Where foliar sprays are useful, it would be well to test acidification plus the inclusion of surfactant as a procedure for more effectiveness and less phytotoxicity.

TRUNK INJECTIONS

Injection of tree trunks with solutions of Fe sources also has been tested with varying degrees of success. Trunk damage may occur at the injection sites, leading to increased disease susceptibility. Fall plus spring trunk injections of 1% $FeSO_4$ solutions in apple and pear trees corrected Fe chlorosis for 3 to 4 years (Raese *et al*., 1986).

Pressure injection of very small amounts (2.5 to 5 g per tree) of Sequestrene 138-Fe into avocado trunks produced a very rapid response (Kadman and Cohen, 1973-74). Similar results were obtained by Kadman and Lahav (1982) with injection of 100 ml of either 1% FeEDDHA or 2% $FeSO_4$ solution to the trunk or main branches of chlorotic avocado trees. The duration of the effect was, however, in most cases relatively short, and more than one injection per tree seems to was needed to ensure good distribution of the material throughout the tree. The pressure injection method could be beneficial where rapid response is required, especially in severely iron-deficient chlorotic trees, but it should be followed by soil treatment to provide more durable effects.

Injection of ferric ammonium citrate, via slant drilling of small holes in trunks has also effectively corrected Fe chlorosis. Ferric ammonium citrate is more soluble than Fe sulfate, and 10 ml of a solution with 8% Fe contains enough Fe to increase leaf concentration in 16 kg of leaves by 50 49.9^{-1} expressed on a dry-weight basis; this would be a moderately large tree (Wallace, 1991). One disadvantage of trunk injections could be the risk of over treatment because of high concentrations of Fe applied. Iron toxicity may produce symptoms similar to iron deficiency; however, in the former, symptoms occurred first on lower (oldest) leaves in potted plants (Albano *et al.*, 1996).

DRIP IRRIGATION

Trickle irrigation is perhaps the most convenient and efficient way to apply FeEDDHA because it goes directly to areas of the soil where there is a proliferation of roots. Since drip or sprinkler irrigation is used for relatively high-value crops (e.g. avocado), the 2 to 5 $kg \cdot ha^{-1}$ FeEDDHA that may be needed should be economically acceptable. A common practice in avocado orchards planted on calcareous soils in Israel is to supply 1 a 2 $mg \cdot liter^{-1}$ of FeEDDHA plus surfactant via the water of the irrigation system (Kadman and Lahav, 1982).

Application of mineral acids may efficiently prevent or correct lime-induced chlorosis with drip irrigation. Good results have been obtained with a mixture of HNO_3, H_3PO_4, HCl, and H_2SO_4 via drip irrigation in pears (Janjic and Olar, 1987, cited by Wallace, 1991). The irrigation system would have to be resistant to the acids, but urea, H_2SO_4 and K_2SO_4 may be effective, non-corrosive acidifiers.

ORGANIC MATERIALS AS CARRIER OF IRON FERTILIZERS

Organic sources can prevent or correct lime-induced chlorosis in avocado in two major ways. One is through the chelating ability of the organic matter. Iron as $FeSO_4$ may be added to the organic source, and the chelators may be recycled to supply Fe to plant roots. Also, organics are carriers of Fe in an exchangeable form; so they maintain the pH of the organics in a physiological pH range (slightly acid). Roots are then free to grow into the lime-free organic matrix and absorb needed Fe. In citrus, good results occurred with about 1 $t \cdot ha^{-1}$ of the Fe-enhanced organics (Horesh *et al.*, 1986). The organic matter would minimize inactivation of the Fe and acids by the lime in soils, but not inactivation caused by bicarbonate in irrigation water. High bicarbonate waters would require higher levels of organic-acid-Fe applications.

Iron-deficiency tolerant rootstocks

The avocado apparently exhibits extreme inefficiency in strategy I mechanism of iron uptake, although this has not been demonstrated. However, differences in susceptibility exist among and within horticultural races used as rootstocks (Wallace and Lunt, 1960).

Genetic variation may be very important in avocados grown under stressful conditions. Leaf Fe concentration of West Indian (WI) avocado seedlings growing under progressive soil salinity was significantly greater (254 $\mu g \cdot g^{-1}$) than for Guatemalan (G) and Mexican (199 $\mu g \cdot g^{-1}$) races (Solares-Morales *et al.*, 1984a). However, significant variation exists among the seedlings originating from a single open-pollinated mother tree. This variability was greater for WI seedlings than for seedlings of either the Mexican race or “chinini” (*Persea schiedeana* Nees) (Solares-Morales *et al.*, 1984b). Differences among races and seedlings origin also occurred in avocado seedlings grown in calcareous soils (López-Jiménez, 1985).

In Israel, WI seedlings of the “Nachlat” group, and trees grafted on such seedlings rootstocks, have shown the highest tolerance to calcareous soils (Ben-Ya’acov, 1977), while rootstocks of the WI x G hybrids (‘Hall’, ‘Fuchs’, ‘Booth 8’) exhibited a great range of levels of chlorosis (Kadman and Ben-Ya’acov, 1982). Rootstocks of Mexican and Guatemalan race origin were much more susceptible to chlorosis than the West Indian and some of their hybrid rootstocks, although some exceptional individual trees of the Mexican race, such as ‘G.A. 13’ or ‘G.L. 7’, showed outstanding tolerance (Kadman and Ben-Ya’acov, 1980a). An excellent representative of the “Nachlat” group is ‘Maoz’ (Kadman and Ben-Ya’acov, 1980b). This and other WI rootstocks are used today on a large scale in commercial avocado orchards in soils containing 50% or more $CaCO_3$ (Kadman and Ben-Ya’acov, 1982). A large-scale selection program for the adaptation of rootstocks for soils of higher lime content is being continued in Israel.

The apparent solution for growing avocado trees under adverse soil conditions, such as high lime content, is to use tolerant rootstocks, rather than to treat the trees after the damage has occurred. Considerable genetic variation exists for tolerance to lime-induced chlorosis. High genetic variation by place of origin provides an excellent opportunity to detect outstanding genotypes adapted to different environmental conditions, including alkaline and calcareous soils. Development of more Fe-efficient cultivars or rootstocks still appears to be the best strategy to control Fe chlorosis. Perhaps the techniques of molecular biology may be beneficial in developing cultivars that are more Fe-efficient or exhibit a greater Fe-stress response.

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